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ORIGINAL PAPER

Morphological study of the labial sensilla in Nabidae (Hemiptera: Heteroptera: Cimicomorpha)

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Abstract

The study presents new data on the morphology and distribution of the labial tip sensilla of six species of two nabid subfamilies—Protosteminae and Nabinae (Heteroptera: Cimicomorpha), which were obtained using a scanning electron microscope. In both taxa, there are five morphologically distinct types of sensilla on the tip of the labium: peg sensilla with a terminal pore, nonporous peg sensilla, elongated placoid sensilla with wall pores (multiporous), and trichoid sensilla. In addition, oval plate sensilla with a terminal pore (Tp-opls) were observed in the genus *Himacerus*. Campaniform sensilla and nonporous chaetic sensilla were observed on the surface of the last segment of the labium in all of the studied species. Over a dozen trichoid sensilla were scattered on the last segment of the labium only in the genus *Prostemma*. Based on their external structure, it is likely that these sensilla are chemosensitive and mechanosensitive. The oval plate sensilla with a Tp-opls (gustatory) in *Himacerus* (Nabinae) represent a morphological novelty that probably evolved independently of other nabids.

Keywords True bugs · Damsel bugs · Morphology · Labium · Scanning electron microscope

Introduction

According to the combined morphological and molecular analysis by Schuh et al. (2009), Nabidae (damsel bugs) belong to the infraorder Cimicomorpha and the clade Cimiciformes. Views on the relationships between and within the groups that belong to this clade are varied and unclear (Schuh and Slater 1995; Schuh et al. 2009). Kerzhner (1981) recognized four subfamilies of Nabidae: Nabinae, Prostemminae, Velocipedinae, and Medocostinae. The first two subfamilies belong to the Nabidae, whereas the systematic positions of the Velocipedinae and Medocostinae have recently been recognized as being separate families (Schuh et al. 2009) and this concept has been adopted in this study. Damsel bugs include approximately 20 genera and 500 species, which are distributed worldwide from about 70°N to 56°S (Schuh and Slater 1995; Kerzhner 1996). In the Palearctic, there are 111 species that are classified into nine genera and two subfamilies—Nabinae A. Costa, 1853 and Prostemmatinae Reuter, 1890 (Kerzhner 1996). Forty-two species from five genera occur in Europe (Aukema 2013).

Most species are of a moderate size and only exceed 10 mm in length occasionally. Many are elongated and have a drab coloration, whereas others are more stout-bodied and occasionally have distinctive red and black color patterns (Schuh and Slater 1995).

Both the larvae and adults of all of the representatives are predators of insects and other small arthropods and feed on their eggs, larvae, and imagines. Most species are polyphagous, but Prostemmatinae are specialized predators of bugs, especially of Lygaeidae (Latin 1989; Kerzhner 1996). The puncture of plants tissues is exceptional and is only used for rehydration, but no development follows (Péricart 1987; Stoner 1972; Lattin 1989).

Although all Prostemmatinae and some Nabinae are ground inhabiting (in litter, under stones, etc.), most Nabinae are herbicolous and some are arboricolous. The humidity requirements vary depending on the type and species (Péricart 1987; Kerzhner 1996). The representatives of the subfamily Prostemmatinae have relatively narrow ecological requirements and prefer xerothermic habitats, while Nabinae have a much broader range of preferences (Péricart 1987).

Nabidae play a significant role in maintaining the biological balance of the environment. Common and numerous

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species of Nabinae are important for controlling agricultural and forest pests (Kerzhner 1996); however, due to their polyphagy, cannibalism, and their variation in numbers over time and space, they are not suitable for the natural control of pests (Cmoluchowa 1978; Lattin 1989).

The feeding of the various zoophagous species of nabids is controlled by sensilla, which are situated in sensory fields on the labial tip. Predatory Heteroptera, e.g., damsel bugs, prefer large, soft-bodied prey in which blood turgor may influence the feeding rate (Cobben 1978). Different types of cuticular sensilla that discriminate complex chemical and mechanical stimuli occur on various areas of the labium, so different types of labial sensilla (chemo- and mechanosensilla) have been recorded in many species of Heteroptera: Nepomorpha (Benwitz 1956; Lo and Acton 1969; Cobben 1978; Jarial 2003; Brożek 2008, 2013), Gerromorpha (Cobben 1978; Brożek and Zettel 2014), Pentatomomorpha (Schoonhoven and Henstra 1972; Khan 1972; Peregrine 1972; Gaffal 1981; Usha Rani and Madhavendra 1995; Ventura et al. 2000; Ventura and Panizzi 2005; Wang and Dai 2017), and reduviids of the Cimicomorpha (Bernard 1974; Catalá 1996; Rosa et al. 1999; Brożek and Chłond 2010). In many hemipteran species, a great diversity and abundance of sensilla on the labium has been observed. The morphological characteristics of the labial sensilla and their distribution have permitted the specific pattern of the labial sensilla to be established in the studied taxa. In Reduviidae (Triatominae and Peiratinae), it was suggested that the interspecific diversity and intraspecific similarity in the shape and numbers of labial sensilla can be used as taxonomic characters (Catalá 1996; Brożek and Chłond 2010).

The rostrum of representatives of Nabidae is flexible and very mobile; it is composed of four segments and never exceeds the mesocoxae in the resting position. The first article is rectilinear and thick, while the third is generally the longest. The first two joints are the most flexible. The mandibular stylets, which are finely denticulate, are shorter than the maxillary stylets, which have sharp denticles, which are directed forward in their anterior region (Péricart 1987).

Detailed morphological descriptions of the labial types of sensilla in the nabid species have never been reported. We can expect them to be similar to other cimicomorphan species as well as to other heteropteran species that have various feeding modes. We decided to conduct a morphological study of the labial tip sensilla of Nabidae to determine the significance of their diversity.

The aim of this study was to find the characteristic set of labium traits in Nabidae. The objectives included: (1) determining whether there are differences in the structure, distribution, and number of the labial tip sensilla in Nabinae and Prostemmatinae as well as between the genera and species within them and (2) attempting to identify the probable functions of the sensilla.

Materials and methods

Materials examined

The study is based on dry material that came from the collection of the Department of Zoology, Faculty of Biology and Environmental Protection, University of Silesia in Katowice (DZUS). Five species that are common in Central Europe belong to two genera of Nabinae: *Himacerus* (*Himacerus*) *apterus* (Fabricius, 1798) (Fig. 1a), *Himacerus* (*Aptus*) *mirmicoides* (O. Costa, 1834) (Fig. 1b), *Nabis* (*Nabis*) *brevis*

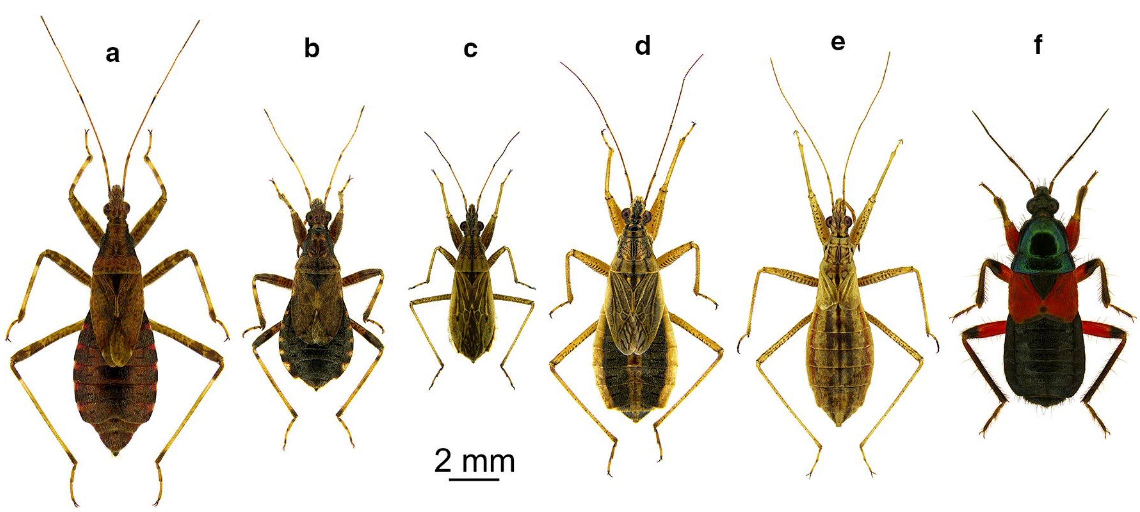

Fig. 1 Habitus of the examined species: **a** *Himacerus apterus*; **b** *Himacerus mirmicoides*; **c** *Nabis brevis*; **d** *Nabis flavomarginatus*; **e** *Nabis limbatus*; **f** *Prostemma guttula* (according to Gierlasiński and Taszakowski 2018)

Scholtz, 1847 (Fig. 1c), *Nabis* (*Nabicula*) *flavomarginatus* Scholtz, 1847 (Fig. 1d), and *Nabis* (*Dolichonabis*) *limbatus* Dahlbom, 1851 (Fig. 1e). The final studied species was a representative of the Prostemmatinae subfamily—*Prostemma guttula* (Fabricius, 1787) (Fig. 1f).

Scanning electron microscopy

All of the Nabinae material (heads of insects) were dissected and cleaned in detergent using an ultrasonic cleaner. Due to the large amount of dirt, the *Prostemma guttula* specimen was cleaned according to the protocol for fixation and was cleaned with KOH (Schneeberg et al. 2017). Then, the method described by Kanturski et al. (2015, 2017) was followed: dehydration using serial baths of 80%, 90%, and 96% ethanol for 20 min each and two baths of absolute ethanol for 30 min each. The basal part of the head with the labium was glued onto the stage of a scanning microscope, coated with a film of gold, and photographed with a Phenom XL (Phenom-World B.V., Eindhoven, The Netherlands) and Hitachi SU8010 (Hitachi, High-Technologies Corporation, Tokyo, Japan) scanning electron microscope in the scanning microscopy laboratories of the Faculty of Biology and Environmental Protection of Silesian University in Katowice. The color photographs were obtained using graphic editor Adobe Photoshop CS6.

Terminology for the sensilla

The terminology and classification of the apical labial sensilla is mainly based on the morphological criteria of sensilla that was established by Altner and Prillinger (1980), Zacharuk (1980), Brożek and Bourgoin (2013) and Brożek and Zettel (2014).

For a description of the sensilla in the figures, we decided to use colors according to the legend attached to each figure rather than the abbreviations that are standard in this type of work.

Results

Two rounded apical lobes of the last segment of the labium form the labium tip and the lobes lie laterally to the dorsal stylet groove (Fig. 2a, 3). On each lobe, a mixed population of sensilla forms a sensory field.

Seven morphologically distinct types of sensilla were identified: peg sensilla with a terminal pore (Tp-ps); nonporous peg sensilla (Np-ps); elongated placoid sensilla with wall pores (multiporous), (Wp-ples); oval plate sensilla with a terminal pore (Tp-opls), nonporous chaetic sensilla (Np-chs), nonporous trichoid sensilla (Np-ts), and campaniform sensilla (CS). These sensilla were functionally recognized as

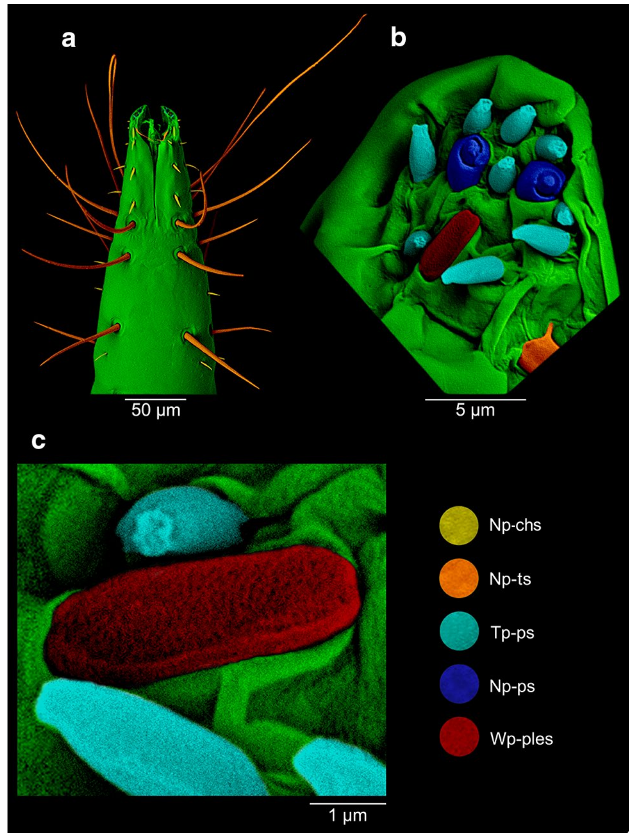

Fig. 2 **a–c** *Prostemma guttula*

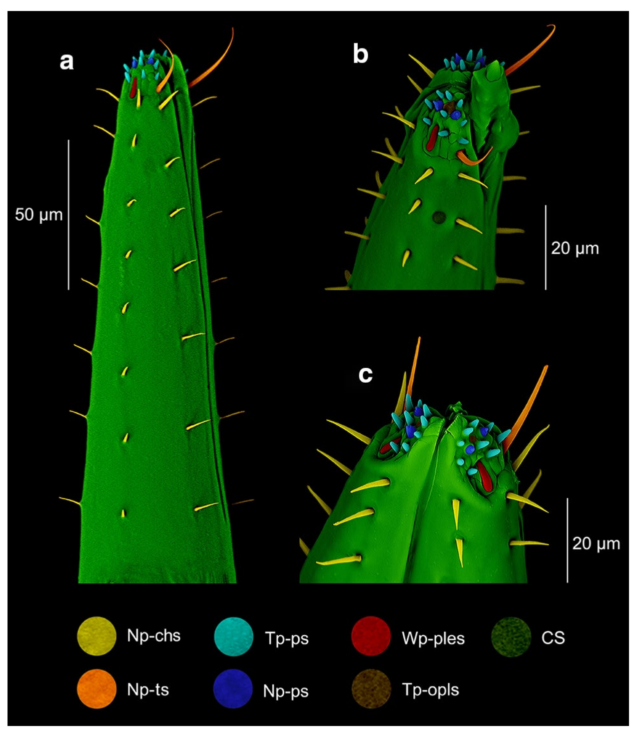

Fig. 3 **a**, **b** *Himacerus mirmicoides*; **c** *Himacerus apterus*

being mechanosensilla, chemosensilla (gustatory and olfactory), and thermo-hygrosensilla.

Types of sensilla

Nonporous trichoid sensilla (*Np-ts*)—smooth and hair-like mechanosensilla arising from flexible sockets. This was the longest type of sensilla that were present on the labium of the examined species. Trichoid sensilla were softer and more flexible than chaetic sensilla. Two sensilla were present in the lower ventral part of the labial tip in *Prostemma*, *Nabis,* and *Himacerus* (Figs. 2a, 3a–c).

Nonporous chaetic sensilla (*Np-chs*)—smooth or ribbed mechanosensilla, hair-like structures arising from flexible sockets. This was the second longest type of sensilla that were present on the labium of examined species (around 7.8 µm). They were less flexible than trichoid sensilla, rigid, and sharpened at the tip. They covered the surface of the entire labium except for the tip. Sensilla were arranged regularly along the entire length (Figs. 2a, 3a–c).

Nonporous peg sensilla (*Np-ps*) (= *aporous styloconic sensillum*)—these were short cones that arose from inflexible sockets. The base of the sensillum with the socket grew over

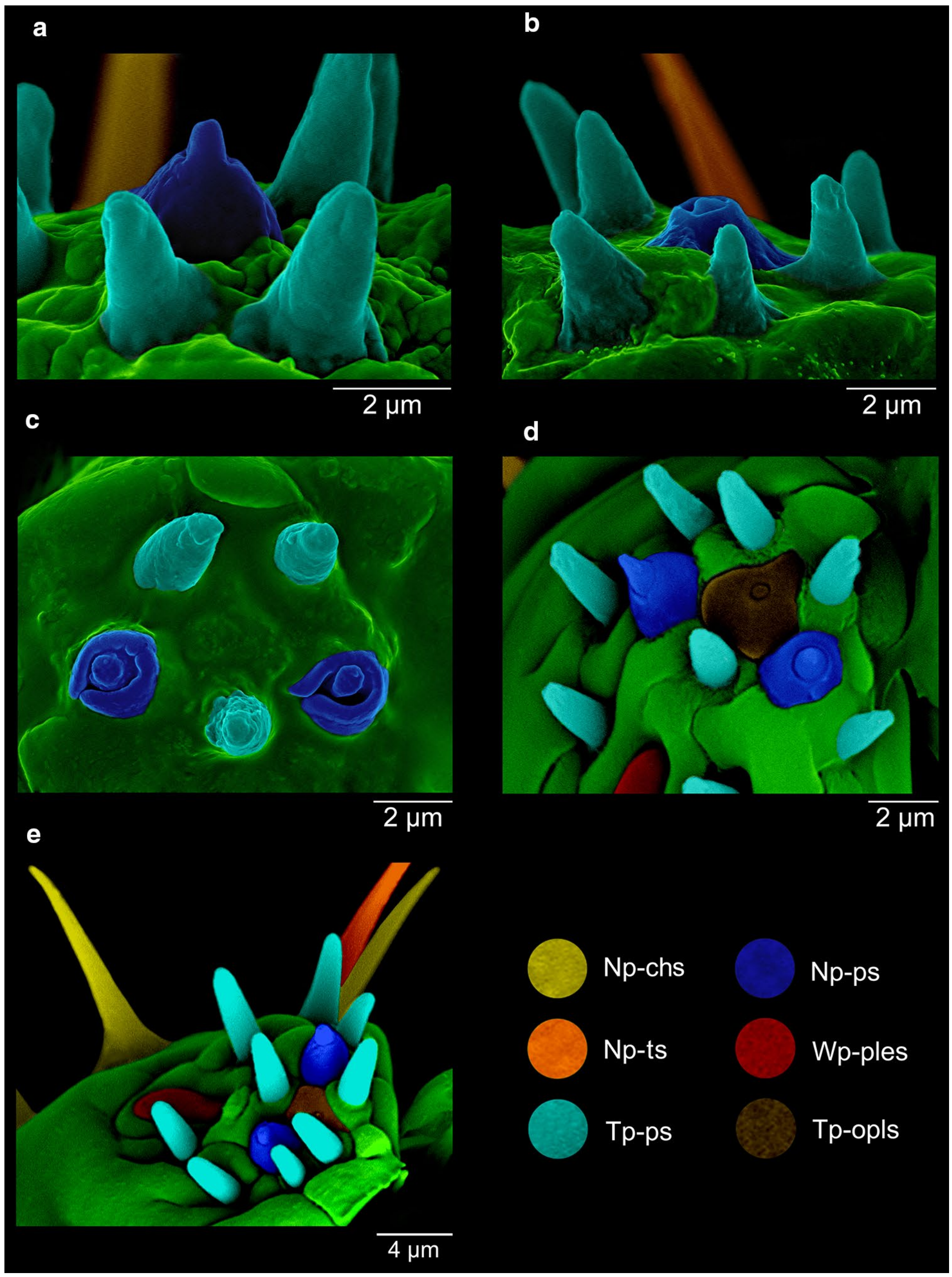

Fig. 4 **a** *Nabis brevis*; **b**, **c** *Nabis flavomarginatus*; **d** *Himacerus mirmicoides*; **e** *Himacerus apterus*

the cuticle. A sensillum could either grow over the socket or remain hidden inside the base. They occurred at the tip of the labium and two sensilla were usually present on each side (Figs. 2b, 3a–c, 4a–e, 5b) in *Prostemma*, *Nabis,* and *Himacerus*.

Peg sensilla with a terminal pore (*Tp-ps*)—short cones with a single pore at the tip of a sensillum arising from inflexible sockets. They occurred in groups (nine sensilla) on each side of the labium. They were only present at the tip, and functionally, they belonged to the gustatory or contact chemoreceptive sensilla (Figs. 2b, 3a–c, 4a–e) in *Prostemma, Nabis,* and *Himacerus.*

Oval plate sensilla with a terminal pore (*Tp-opls*)—these were placoid sensilla, although they only had one terminal pore. They arose from inflexible sockets, were present at the tip of the labium and surrounded with Tp-ps and Np-ps sensilla. There were two sensilla present, one on each side of the labium. This type of sensilla was only found in *Himacerus* (Figs. 3b, c, 4d, e).

Placoid elongated sensilla with wall pores (*Wp-ples*)—these were elongated oval plates that had multiple pores (Figs. 2b, c, 3a–c, 4d, e, 5a). They are considered to be chemosensilla (olfactory). They arose from inflexible sockets. There were the only two placoid sensilla present on the tip of the labium, one on each side (Fig. 3c) in all of the studied species.

Campaniform sensilla (*CS*)—flat, oval disks with a single pore on their surface. They were socked in flexible sockets. A single sensillum occurred along the length of the labium of *Himacerus mirmicoides* (Figs. 3b, 5c) and probably also in other species.

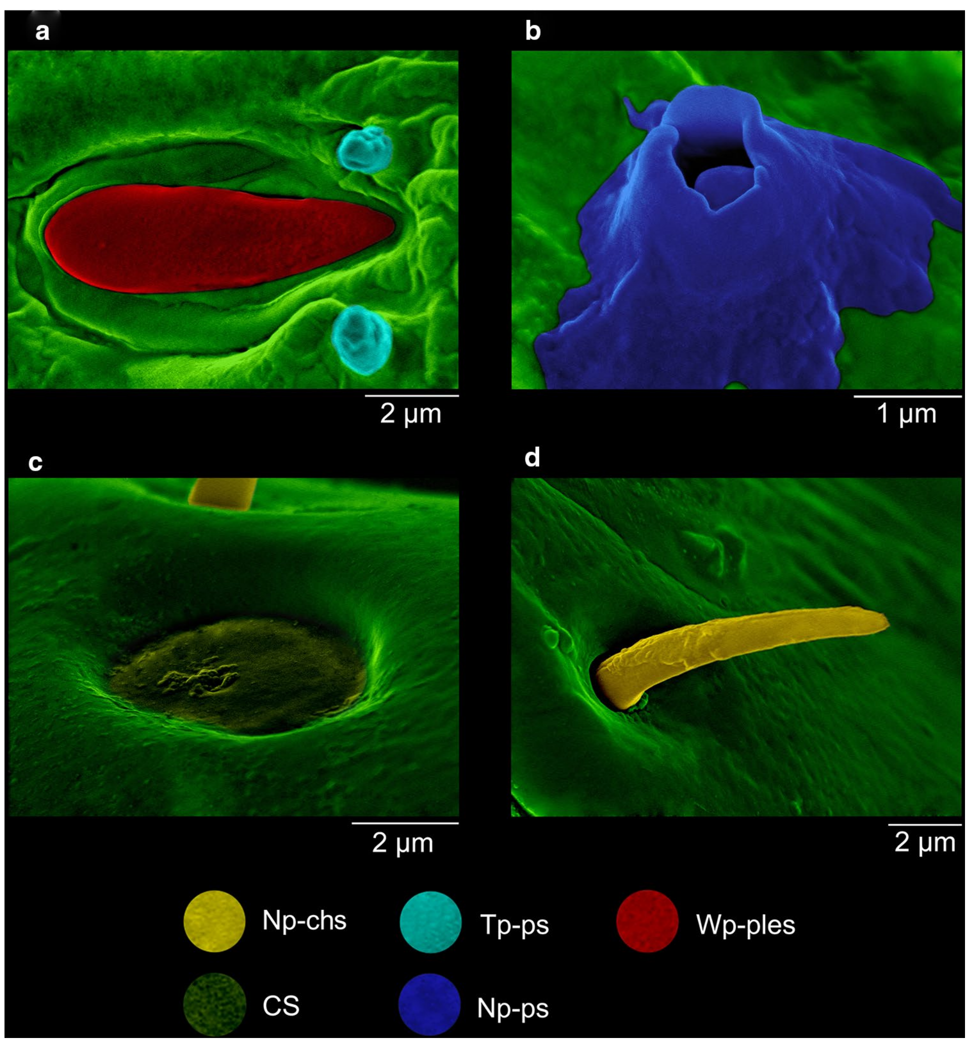

Fig. 5 **a** *Nabis brevis*; **b–d** *Nabis flavomarginatus*

Discussion

The diversity of labial sensilla in bugs is inextricably connected with the diversity in the feeding behavior and evolutionary pressure on the bugs that are observed in specific taxa, and this has been the subject of long-standing interest in morphological and functional research. Moreover, this diversity of sensilla in many insects is a potentially valuable information source for reconstructing their phylogeny (Faucheux et al. 2006).

In many different species of Heteroptera that are characterized by different feeding behaviors, the labial sensilla have been studied by many authors (Beck et al. 1958; Schoonhoven and Henstra 1972; Peregrine 1972; Cobben 1978; Avé et al. 1978; Gaffal 1981; Backus 1988; Usha Rani and Madhavendra 1995; Ventura et al. 2000; Ventura and Panizzi 2005; Brożek 2008, 2013; Brożek and Chłond 2010; Brożek and Zettel 2014; Parveen et al. 2015; Wang and Dai 2017). In all of the analyzed species, it has been stressed that the labial tip sensilla are similar and that a common pattern can be established for species that belong to the same family or group of families that are closely related and that prefer the same kinds of food. The slightly visible difference in the numbers and type of sensilla may result from different feeding. This phenomenon was observed between phytophagous and zoophagous pentatomids, because these predators had two types of chemoreceptive sensilla (peg and styloconic) on the labial tip, whereas only one type of chemoreceptive sensilla (peg) occurred in phytophagous representatives (Parveen et al. 2015).

From previous studies, a substantial amount of information on the labial sensilla in Gerromorpha, Nepomorpha, and most species of Pentatomomorpha is available (comprehensive reviews by Cobben 1978; Brożek and Zettel 2014; Brożek 2013; Parveen et al. 2015; Wang and Dai 2017). Among the studied taxa of Cimicomorpha, the family Nabidae has been poorly described in the recent studies. Sinitsina and Chaika (1997) in *Nabis flavomarginatus* (Scholtz, 1847) noticed 11 sensilla on the labial tip—nine short basiconic sensilla and two papillae. Although the placoid elongated sensillum with wall pores (Wp-ples) is visible in Fig. 2e in the paper of the above-mentioned authors, no information about this sensillum was found in the description and discussion parts. In the present study, we conducted a comparative analysis of the labial tip sensilla and the distribution of different types of sensilla on the surface of the last segment of the labium in Nabidae (Prostemminae and Nabinae).

Pattern of labial tip sensilla

In Nabidae, two lobes of the labial tip have two identical sensory fields that are equipped with chemosensilla of three morphological types, which presumably function as gustatory—nine peg (Tp-ps) and one plate (Tp-opls), and olfactory—one placoid (Wp-ples) (Table 1). Moreover, the sensory fields also include a thermo–hygroreceptive sensilla (two short pegs Np-ps) and one nonporous trichoid sensillum (Np-ts). Consequently, in Nabidae, two patterns of labial tip sensilla can be distinguished. The first pattern had 13 sensilla (nine Tp-ps + two Np-ps + one Wp-ples + one Np-ts) on each lobe and was characteristic for *Prostemma* and *Nabis*. The second one consisted of 14 sensilla (nine Tp-ps + one Tp-opls, two Np-ps + one Wp-ples + one Np-ts) and was only observed in *Himacerus*.

In the other groups of Cimicomorpha, e.g., Reduviidae and Miridae, which are not closely related to Nabidae (Schuh et al. 2009), the numbers and types of labial tip sensilla were essentially different among them, even in the predatory taxa, and were similar to those in Nabidae. In 19 species of predatory Reduviidae (Peiratinae), the set of labial tip sensilla was different from Nabidae and was usually formed by five Tp-ps and one or two Np-ps and, moreover, the Wp-ples were singularly located distally on both sides of the tip of the last segment (Brożek and Chłond 2010).

A nonporous peg sensilla (= poreless coeloconic sensilla) was present only on the labial tip in nabid species, whereas

Table 1 Functional sensilla types

Species	Characteristic				
	Gustatory	Gustatory	Olfactory	Thermo–hygroreceptors	Mechanoreceptors
	Uniporous peg (Tp-ps), inflexible socket	Uniporous plate (Tp-opls), inflexible socket	Multiporous placoid (Wp-ples), inflexible socket	Smooth surface (Np-ps), inflexible socket	Nonporous, (CS), (Np-ts), (Np-chs), flexible socket
P. guttula	Tp-ps	–	Wp-ples	Np-ps	(CS), (Np-ts), (Np-chs)
H. apterus *H. mirmicoides*	Tp-ps	Tp-opls	Wp-ples	Np-ps	(CS), (Np-ts), (Np-chs)
N. flavomarginatus *N. limbatus* *N. brevis*	Tp-ps	–	Wp-ples	Np-ps	(CS), (Np-ts), (Np-chs)

such sensilla are scattered on the surface of the apical labial segment in other taxa, e.g., Peiratinae: *Peirates hybridus* (Scopoli, 1763), *Lamotteus ornatus* Villiers 1948, *Thymbreus crocinopterus* Stål, 1863, *Brachysandalus bicolor* Villiers, 1948, and *Melanolestes picipes* (Herrich-Schaeffer, 1846) (Brożek and Chłond 2010).

In hematophagous reduviid species, such as *Triatoma sordida* (Stål, 1859), *T. platensis* Neiva, 1913, *T. protracta* (Uhler, 1894), *T. infestans* (Klug, 1834), *T. guasayana* Wygodzinsky & Abalos, 1949, *T. circummaculata* (Stål, 1913), and *T. rubrovaria* (Blanchard, 1843), the morphology of the labial tip sensilla suggests taste (porous pegs) and thermo-perception (pegs in pits) (Catalá 1996; Rosa et al. 1999). However, the number of these sensilla in the above-mentioned taxa was not provided. Nevertheless, in *Triatoma* species, the multiporous sensillum does not belong to the formula of labial tip sensilla, because it is situated distally on the lateral side of the labial tip as in Peiratinae, which distinguishes both of these taxa from Nabidae.

The hematophagous bed bug (*Cimex hemipterus* Fabricius, 1803) (Cimicidae) has a few sensilla on the rostral tip, which are likely to be olfactory sensilla and more than 20 argyrophilic basiconic-like pegs, which are likely to be gustatory sensilla. Most of the other hairs are mechanosensilla (Singh et al. 1996). Despite the fact that Nabidae are in a close relationship with Cimicidae (Schuh et al. 2009; Johnson et al. 2018), the patterns of labial tip sensilla in both taxa are evidently different, because olfactory basiconic sensilla have been reported in *C. hemipterus*, whereas olfactory placoid elongated sensilla with wall pores (Wp-ples) have been reported in nabid species.

In turn, in the phytophagous species *Lygus rugulipennis* Poppius, 1911 and *L. lineolaris* (Palisot de Beauvois, 1818) (Miridae), 11–12 uniporous gustatory peg/basiconic sensilla and one nonporous mechanoreceptor are situated ventrally on both areas on the tip of the labium (Avé et al. 1978; Hatfield and Frazier 1980; Romani et al. 2005). Moreover, Wp-ples were observed in a few taxa of mirids (data unpublished, A. Taszakowski). The pattern of the labial tip sensilla in mirids is similar to the one in nabids. Even in taxa that are more distant in relation to Nabidae, the labial tip sensilla show a certain degree of similarity, which has been observed, for example, in the seed bug *Pyrrhocoris sibiricus* Kuschakewitsch, 1866. The latter taxon has 12 thick-walled 'uniporous sensilla basiconica IV', but two of them are shorter and are embedded in higher sockets (no. 9 and 10) (Wang and Dai 2017). Sensilla basiconica IV correspond to the Tp-ps in nabids and sensilla no. 9 and 10 appear to be identical to Np-ps in nabids. However, the main difference compared to Nabidae is the lack of Wp-ples on the labial tip in seed bugs as well as in other pentatomomorphan bugs such as *Nezara viridula* (Linnaeus, 1758) (Pentatomidae) (Usha Rani and Madhavendra (1995), *Dolycoris indicus* Stål, 1876, *Plautia crossota* (Dallasi, 1851), *Piezodorus hybneri* (Gmelin, 1790), *Perillus bioculatus* (Fabricius, 1775) and *Eocanthecona furcellata* (Wolff, 1811) (Parveen et al. 2015), *Dysdercus fulvoniger* (De Geer, 1773), *D. koenigii* (Burmeister, 1835), *D. fasciatus* Signoret, 1861, *D. intermedius* Distant, 1902 (Pyrrhocoridae), *Blissus leucopterus* (Say, 1832) (Baker et al. 2008), and lygaeid *Elasmolomus pallens* (Dallas, 1852) (Usha Rani and Madhavendra 2005). Moreover, in the aforementioned species, there are different numbers of gustatory peg/basiconic sensilla or contact chemoreceptors (basiconic or trichoid sensilla) that range from 12 to 16 (Schoonhoven and Henstra 1972; Peregrine 1972; Gaffal 1981; Parveen et al. 2015) in contrast to Nabidae, which has ten gustatory sensilla. Usually, one or two nonporous mechanoreceptors are located ventrally on both areas of the labium tip in most pentatomomorpha taxa, which is similar to nabid species.

Sensory system of the labial tip

The rostrum in Nabidae has sensilla with four modalities: olfactory, gustatory, thermo-hygroreceptors, and mechanosensory. At the distal tip of the rostrum, there are two sensilla pegs (similar to coeloconic sensilla), which are probably thermo-hydrophilic. The Tp-opls (gustatory) in *Himacerus* (Nabinae) represent a morphological novelty that probably evolved independently of other nabids within the context of the functional mechanism of nutrition of this predator. At present, it is known that *Prostemm*a, *Nabis,* and *Himacerus* feed in the same manner; however, they have a different labial sensilla complex that consists of one type of gustatory sensilla in *Prostemma* and *Nabis* and two types of gustatory sensilla in *Himacerus*. It can be assumed that the additional plate sensillum in *Himacerus* is crucial for efficiently probing prey, which is similar to the sensilla of the labial tip in zoophagous pentatomids (Parveen et al. 2015). Different gustatory sensilla (most of which are dome-shaped) were observed in predatory gerromorphan species and a special plate triangular sensillum with a terminal pore was also observed only in Rhagadotarsinae from among several gerromorphan taxa that were studied (Brożek and Zettel 2014).

The data of the several gustatory sensilla from the labial tip are in accordance with previous studies of hemipterans and other insects, thus suggesting a conserved gustatory coding mechanism among the various taxa. For most of the studied species of Heteroptera (Nepomorpha, Pentatomomorpha) (Pentatomidae, Pyrrhocoridae), Cimicomorpha (Reduviidae, Miridae), peg, papillae, basiconic, or oval plate sensilla with a terminal pore on the labial tip are responsible for the gustatory function (Cobben 1978; Avé et al. 1978; Peregrine 1972; Gaffal 1981; Walker and Gordh 1989;

Catalá 1996; Romani et al. 2005; Brożek and Chłond 2010; Brożek 2013).

Insects have gustatory systems that allow them to distinguish between a host and non-host. The presence of a single pore at the tip of the sensilla suggests that they have a chemical function (gustatory) or that they are contact chemoreceptors (Altner and Prillinger 1980; Zacharuk 1980; Chapman 1995, 1998; Shields 2010).

The food selection behavior of other insects is predominantly governed by the activation of the taste neurons that are present in styloconic sensilla, peg sensilla or other morphological types of sensilla that are situated on the labial tip like in the hemipteran species as well as on the other parts of proboscis, e.g., sensilla on the galea of the maxilla of Lepidoptera (Mitchell et al. 1999; Schoonhoven and Dethier 1966; Schoonhoven et al. 2005; Chapman 1998).

The labial olfactory system in Nabidae is weakly developed and is served by one large Wp-ples that was present in all of the studied species.

Np-ps correspond to the morphological character of the same sensilla peg type 2 on the labial tips of pentatomid species (Parveen et al. 2015) and have been mentioned as being sensilla that have a chemical function in *Pyrrhocoris sibiricus* (Wang and Dai 2017). This type of sensilla also conforms to this scheme of the sensillum in other insects, which are also called nonporous styloconic sensilla (Faucheux et al. 2006). Furthermore, the fine structure of thermo–hygroreceptive sensilla seems to be conserved throughout the insect orders (Altner et al. 1983; McIver 1973; McIver and Siemicki 1976; Steinbrecht and Müller 1976; Venkatesh and Singh 1984; Yokohari 1981, 1983).

Mechanosensilla of the last segment

The last segment in studied species of Nabidae has three types of mechanosensilla (trichoid, chaetic, and campaniform). A distinct difference was observed in the length and quantity of Np-ts in *Prostemma*. They were significantly longer and more numerous than in the *Nabis* and *Himacerus* species. Usually, long Np-ts were more or less numerous and occupied a position near labial tip ventrally and dorsally.

In Miridae (*Lygus rugulipennis* and *L. lineolaris*), two types of trichoid sensilla (nonporous mechanoreceptor) were observed. The first was situated ventrally on both areas of the labium tip, while the second was observed more proximally on the labium (Avé et al. 1978; Romani et al. 2005). The arrangement of these sensilla appears to be similar to *Prostemma*. The functional significance of these sensilla on the labium seems to be clear—it provides information about the position of the labium with respect to the surface of the host.

In the Nabidae species, the size and the arrangement of Np-chs in four rows on the labial segment were identical. The sensilla were short and scattered on the surface. According to Backus (1988), the poreless mechanosensory short or long stiff hairs (chaetic sensilla) along the sides of labium that are usually observed in many hemipterans are responsible for detecting the degree of labial bend when probing. Many data confirm the different shapes and sizes of the mechanosensilla (trichoid, chaetic, and other specific shapes) and their distribution pattern over the labium and an interspecific variability of these sensilla on the rostrum was even found in the hematophagous species of *Triatoma* (Catalá 1996; Rosa et al. 1999). In hemipteran taxa, such studies refer to the labial sensilla in Pentatomidae (Parveen et al. 2015), Pyrrhocoridae (*Pyrrhocoris sibiricus*) (Wang and Dai 2017), in Peiratinae (Brożek and Chłond 2010), in many nepomorphan species (Brożek 2013), in Coccoidea (Tachardiidae) (Ahmad et al. 2012), and in Fulgoromorpha (Brożek and Bourgoin 2013). Depending on their taxonomic position, the pattern distribution of the mechanosensilla was quite different. Differences in the distribution and size of the mechanosensilla (trichoid) were clear between Prostemminae and Nabinae.

In Nabidae, a few campaniform sensilla (CS) were found in some areas on the labium. They were identical to those that were described in Peiratinae (Reduviidae) by Brożek and Chłond (2010) in Pentatomidae (Parveen et al. 2015), and in Pyrrhocoridae (Wang and Dai 2017). They are mechanosensilla that have the function of proprioception, which responds to any strains in the exoskeletons (McIver 1975; Koteja 1980; Chapman 1998).

The studied species have identical types of feeding habits; the sets of labial sensilla were similar, especially the chemosensilla (peg, placoid) and mechanosensilla, which play a role in host selection. Moreover, the specialized Tp-opls recognize the surface of the prey host in the case of predatory *Himacerus*.

Evolutionary aspects of the sensilla

The present comparative investigation is also an attempt to establish the set of the labial-type sensilla in Nabidae and to determine their plesiomorphic and apomorphic character in relation to other cimicomorphan taxa.

The results of the present study indicate that the Prostemminae (*Prostemma guttula*) and Nabinae (*Nabis brevis, N. flavomarginatus, N. limbatus* and *N. flavomarginatus*) represent a common pattern of labial tip sensilla, which is composed of the same types and number of sensilla, except for genus *Himacerus*. The latter taxon has one additional type of sensillum—Tp-opls, which is unknown in other nabids and other cimicomorphan taxa. Possibly, this sensillum constitutes an autapomorphy in *Himacerus* genus.

A plate triangular sensillum with a terminal pore was indicated as being an autapomorphy in the predatory

Rhagadotarsinae (Gerromorpha) (Brożek and Zettel 2014) and is almost the same as in *Himacerus*, which is probably a parallel character for both taxa.

A comparison of Nabinae with Prostemminae led us to conclude that most of the sensilla of Nabidae represent a plesiomorphic condition, whereas the additional Wp-ps have been recognized as an autapomorphy of the genus *Himacerus*. This scenario of the development of the sensilla in *Himacerus* compared to *Nabis* and *Prostemma* involves the gain of one independent feature, and therefore, we regard this evolutionary pathway as being likely.

The monophyly of Cimiciformes (Nabidae, Medocostidae, Cimicidae, Microphysidae, Lyctocoridae, and Joppecidae) has been supported in most studies. Cimiciformes is treated as a sister group of the Miroidea (Miridae + Tingidae) in most analyses (Schuh et al. 2009; Johnson et al. 2018). Based on the available data of sensilla, Miridae (Avé et al. 1978) and Nabidae share the same set of labial tip sensilla, except for Tp-opls, which was only observed in *Himacerus*.

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